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The Feeding Mechanism of Fiddler Crabs, with Ecological Considerations of Feeding Adaptations[1,2]

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(Plate I; Text-figure 1)

Introduction

THE ability of an organism to obtain nutrition from its environment is one of the basic requisites for survival and is thus a factor governing the distribution of animals. Should an animal become uniquely adapted to obtain food in a specific manner, the variety of habitats in which it can live becomes accordingly limited. This study of the feeding mechanism of three species of fiddler crabs, *Uca pugilator* (Bosc), *U. pugnax* (Smith) and *U. minax* (Le Conte), was undertaken to observe feeding adaptations which may contribute to limiting their distribution.

Ecological studies have elucidated the grosser conditions prevailing in typical habitats of *Uca*. Pearse (1914), working at Woods Hole, Massachusetts, and Schwartz & Safir (1915) at Cold Spring Harbor, New York, described the habitat of *U. pugilator* and *U. pugnax*. Both species live centrally between the tide marks, where the substrate consistency permits burrowing. However, *U. pugnax* is limited mainly to the mud or clay areas, while *U. pugilator* lives on a sandy substratum. Gray (1942) studied *U. minax* at Solomons Island, Maryland, and noted that the substratum may vary from sand and mud, to clay, though this crab is mainly limited to habitats of lower salinity. The more comprehensive study of distribution of *Uca*, done in the Georgia salt marshes by Teal (1958), has generally supported these observations.

The same workers have also considered the food material of *Uca*. Both Pearse (1912), then working in the Philippines, and Schwartz & Safir found algae and vascular plant tissue to make up the bulk of the stomach contents in the *Uca* examined, though decayed animal matter and inorganic material were also present. By experimental feeding, Gray found *U. minax* to ingest a wide variety of foods, with the notable exception of putrified material. In controlled experiments, Teal found *U. pugilator* and *U. pugnax* able to live on cultured marsh bacteria.

In regard to the manner in which *Uca* feeds, Pearse (1912) described rather completely the action by which the minor chela passes material into the buccal cavity where the food to be ingested is selected by the mouth parts. Working in Brazil, Matthews (1930) observed *U. leptodactyla,* a small species, to take single grains of sand into the buccal cavity, where adhering organic matter is scoured off and the cleaned grain rejected. This scouring action is achieved by the movement of the second maxilliped endopodites across the bristled endite lobes of the first maxilliped protopodite. Matthews also observed spoon-shaped tips on some medianly-projecting bristles of the second maxillipeds. These bristles have become known as spoon-tipped hairs, mainly through the descriptive work of Crane (1941, 1943). Examining tropical *Uca,* as well as the three species of the northern temperate region, she observed a great number of spoon-tipped hairs in the sand-inhabiting species, while crabs living in muddy habitats have an abundance of woolly hairs on the second maxilliped. She suggested the con-

[1] A portion of the field studies included here were supported by a grant from the National Science Foundation (G-5577); grant administered by Dr. F. John Vernberg. Complete reports of these studies will be made in future papers.

[2] This work was submitted in partial fulfillment of the requirements for the Master's degree in the Graduate School of Arts and Science, Duke University.

nection of such hair modifications with feeding. Altevogt (1957) has compiled a list of crabs which show a similar type of hair modification, which supports Crane's generalization correlating the modification of the second maxilliped hairs with habitat. He observed that the spoon-tipped hairs aided in the ridding of coarse particles from the buccal cavity. He has also contributed to the understanding of the feeding mechanism with his description of the washing of coarse material from the buccal cavity by water from the branchial cavity, while the lighter detritus is suspended in the fluid and adheres to the mouth parts for eventual passage to the mouth.

In this study of the feeding mechanism in *Uca*, the morphology of the mouth parts is described, with composite figures showing their relative positions within the buccal cavity. The various aspects of the sorting process within the cavity are considered in detail. Habitat limitation created by the mode of feeding is examined and species differences in mouth-part structure are analyzed, so that the ecological consequences of such specific adaptation may be considered.

I wish to express my appreciation to Dr. F. John Vernberg, who directed this study, and to Dr. R. H. Siepmann for his translation of the German paper by Altevogt.

Methods of Study

While the grosser aspects of the feeding mechanism were observed in the field with the aid of binoculars, or in aquaria in the laboratory, the more detailed processes occurring within the buccal cavity were observed with a dissecting microscope. Details of the mouth parts and associated hairs were most easily discerned when the crabs were submerged in a pan of water. Since *Uca* is very hardy, the third maxilliped could be excised to permit observation of the actions of the other mouth parts. Careful removal of one or both of the first maxilliped endite lobes permitted similar observations of the appendages more immediate to the mouth. The manner in which the mouth appendages manipulate particles was seen by placing sand grains or pieces of modeling clay on the appendages, while the direction of action of the mouth parts was observed by stimulating them with a probe.

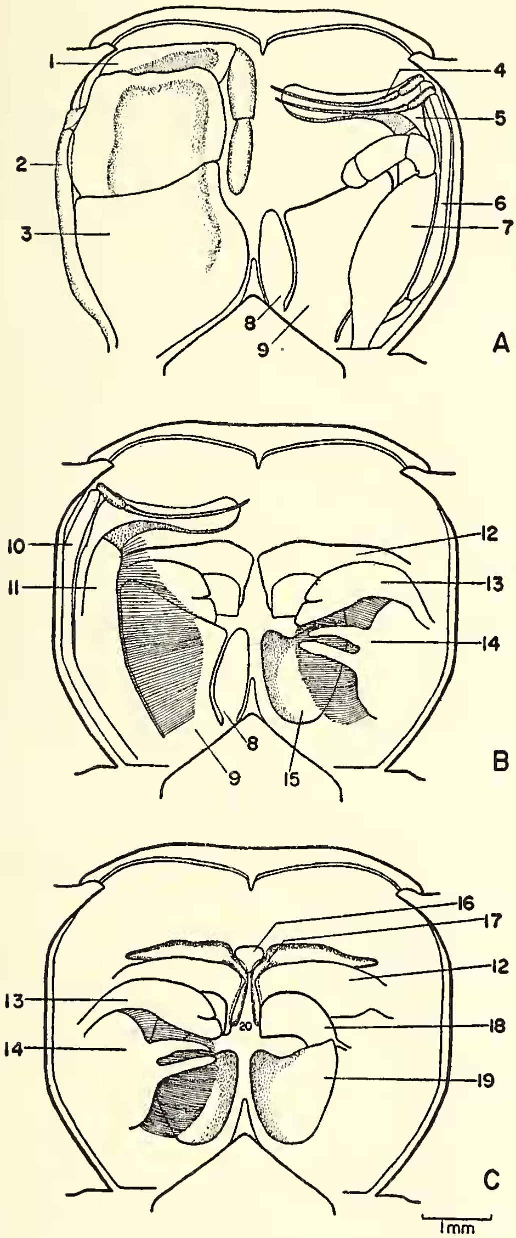
Semidiagrammatic figures of the mouth parts, drawn to show their relative position within the buccal cavity, are included to aid in the understanding of the interrelationship of the appendages. Though the hairs which cover the surfaces of the mouth parts have been generally deleted from the figures for simplicity, these hairs are described in detail in the text.

Observations of the habitats in which the crabs live, as well as the studies of their general distribution, were made during the summers of 1957 and 1958 at Beaufort, North Carolina. The habitats have been characterized by the condition of the substratum, and by the topography and vegetation. Percentage of sand content of the substratum was determined by the hydrometer method as outlined by Bouyoucos (1928).

Appendages and Mouth Structures of the Buccal Cavity

The terminology adapted for description of the mouth parts follows that used by Snodgrass (1950, 1952). However, reference was also made to the general descriptions of crustacean appendages by Siebold (1874), of the Brachyura by T. H. Huxley (1878), and of *Callinectes sapidus* by Lochhead (1950). The appendages are described here with reference to their relative position within the buccal cavity while the crab is in a typical feeding position. At this time the buccal cavity is at a 45° angle in respect to the horizontal, which means that the upper edge of the third maxillipeds can also be termed the anterior edge, and the lower edge, the posterior. These terms are used interchangeably in this discussion.

The third maxillipeds enclose the buccal cavity from beneath. The basal portion of the maxilliped, termed the protopodite, is composed of a coxopodite and a basipodite. An epipodite arises laterally from the coxopodite and extends along the base of the branchiostegite, where it functions as a valve to regulate the intake of respiratory water before it turns into the gill cavity proper. The endopodite and exopodite extend from the basipodite. On the endopodite, the ischiopodite and meropodite are greatly enlarged and join to form a broad plate. The endopodite is bent medially at the fourth joint, to fold the three terminal segments across the meropodite, and finally to extend downward along its median edge as an endognathal palp. The palp is flexible and is used to clean the eyes, antennae and antennules, as well as functioning in the feeding process. The exopodite of the third maxilliped borders the endopodite as a long segment, which terminates as a slender, many-jointed flagellum which extends medially across the buccal cavity. The peduncle of the exopodite shares with the broad plate of each endopodite and their terminal segments to form an operculum across the buccal cavity when the third maxillipeds are closed (Text-fig. 1A). Plumose hairs (setae) fringe the edges of the third maxillipeds, making the appendage more effective as an operculum.



TEXT-FIG. 1. The buccal cavity of *Uca*, ventral view. **A.** The maxillipeds, with the left third maxilliped removed. **B.** Right first maxilliped, maxillae and mandibles. **C.** Right second maxilla, first maxillae, with mandibles in detail. **1**, third maxilliped endognathal palp; **2**, third maxilliped exopodite; **3**, third maxilliped endopodite; **4**, first maxilliped flagellum; **5**, first maxilliped endopodite "flap"; **6**, second maxilliped exopodite; **7**, second maxilliped endopodite (meropodite segment); **8**, first maxilliped coxal endite; **9**, first maxilliped basal endite; **10**, first maxilliped exopodite; **11**, first maxilliped endopodite; **12**, mandible; **13**, second maxilla basal endite; **14**, second maxilla coxal endite; **15**, first maxilla; **16**, anterior lobe of labrum; **17**, mandibular palp (endopodite); **18**, first maxilla basal endite; **19**, first maxilla coxal endite; **20**, month region.

The segmentation of the second maxilliped is similar to the third, though the two basal segments are now united. The endopodite is composed of the five typical segments, but in contrast to the third maxilliped the ischiopodite is fused with the basipodite, and the meropodite is greatly enlongated (Text-fig. 1A). The terminal segments of the endopodite extend medianly from the meropodite, with flexibility similar to those forming the palp of the third maxilliped. The exopodite of the second maxilliped also corresponds with that of the third maxilliped.

The first maxilliped deviates from the general form of the other two maxillipeds as large inward-projecting lobes, or endites, extend from both the coxopodite and basipodite (Text-fig. 1A, B). Short bristles completely cover the outer surfaces of the endites to form a continuous brush-like surface across the lower half of the buccal cavity. The segments of the endopodite extend more along the sides of the cavity, with the meropodite elongated, as in the second maxillipeds, but narrower. A comb, made up of closely set, stout hairs, extends from this segment to lie beneath the bristled endite lobes. The hairs achieve the appearance of a comb due to their close and regular spacing, which is maintained along much of their length by numerous setules along each hair that serve to hold them together on one plane. The fourth joint of the endopodite is again bent, making the terminal segments extend across the buccal cavity. However, in the first maxillipeds, the terminal segments of the endopodites are broad and flattened, so that they appear as flaps. Defining the top of the buccal cavity, the flaps serve to concentrate mineral and food material in the vicinity of the mouth parts. Also, being heavily fringed with plumose hairs, they prevent particulate matter from entering the gill cavities by way of the excurrent openings, which are located immediately above. The exopodite of the first maxilliped is parallel to the endopodite, as described for the other maxillipeds. The terminal flagellum lies, along with the other flagella, across the upper surface of the wide distal portion of the endopodite (Text-fig. 1B). Together, the three pairs of exopodite flagella function to prevent material suspended in the water from entering the excurrent respiratory opening, for by rapid, upward-flicking motions, the flagella can set up currents in the water which carry away such suspended material.

The second maxilla is distinct in form in that a pair of bifid endites extends medianly from the coxopodite and basipodite. The lower, or coxal, endite takes the form of narrow finger-like projections which are relatively devoid of hairs, while the upper, or basal, endite appears as one large lobe, though its primitive bifid condition is noted by a short slit which extends into the endite from its median edge (Text-fig. 1C). A comb, very similar to that of the first maxilliped, arises from the arched base of the coxal endite and extends beneath the bifid endite. The comb, with the endite, underlaps a portion of the first maxilla, while the upper endite lies under the first maxilla basal endite. The endopodite of the second maxilla is present only as a tiny spiked remnant extending from the proximal part of the upper endite. The exopodite has combined with the epipodite to form the long, flattened lobe called the scaphognathite. The lobe extends laterally into the gill chamber, where it acts as a pump, moving respiratory water as the second maxilla oscillates laterally.

On the first maxilla, a relatively large lobe extends medianly from an arm of the coxopodite (Text-fig. 1C). The lobe is covered with fine, short hairs, except at its median edge where the lobe curves strongly upwards toward the mouth; there it is fringed with a few rows of stubby, stout bristles. These bristles are set so that they point upwards at a slight angle towards the mouth. Another arm extends from the coxopodite of the first maxilla, which is regarded as the basipodite. This segment also bears an endite, which underlaps the mandible. The endite is slightly curved to fit the contour of the mandible, and its median edge is armed with stubby, stout bristles similar to those of the coxal endite. The small endopodite appears to be rudimentary here, while the exopodite and epipodite are absent from the first maxilla.

The mandibles extend across the upper portion of the buccal cavity with broad quadrate basal parts carrying the large gnathal lobes which project underneath the mouth. In *Uca*, the biting edges are toothless, giving the gnathal lobes a blunt appearance. However, the lobes narrow down to thin, sharp edges as they curve inwards and the upper side becomes somewhat hollowed. Thus it is possible that the mandibles may be utilized for mastication. A three-segmented palp, made up of the terminal joints of the endopodite, extends along the anterior edge of the gnathal lobe and then turns downward to lie in the hollow above the biting edges of the mandible (Text-fig. 1C). Siebold has suggested that the palps serve as tactile organs for the mandibles. Neither the exopodite nor the epipidite are represented in this appendage. A pair of paragnaths lies above and close to the mandibles and immediately over the mouth. They are flat elongated lobes which project forward from the posterior ends of the lateral mouth folds. They have no musculature, according to Snodgrass (1950), though with their fringe of short plumose hairs they appear as rudimentary mouth parts.

The mouth is a distensible opening above the lower portion of the mandibles. From the top of the mouth arises a triangular - shaped fleshy upper lip, called the labrum, which comes to lie beneath the mouth. A portion of the labrum also projects anteriorly above the mandibles as a small triangular lobe. The two lower sides of the lobe are grooved in such a fashion that the mandibular palps fit into it as they curve around the anterior edge of the mandibles (Text-fig. 1C). Thus, any vertical movement of the palps will cause a corresponding movement of the labrum, an upward movement lifting the labrum away from the mouth opening, while a downward movement serves to partially close the opening. Otherwise the mouth is without modification, but the elastic tissue quickly coalesces to form the tubular esophagus.

The Feeding Mechanism

In feeding, the fiddler crab scrapes the surface of the substratum with the minor chela. Among the mineral particles scooped up are detritus, algae, bacteria and perhaps nematodes. The minor chela carries this material up to the buccal cavity and passes it between the slightly gaping third maxillipeds. Within the buccal cavity, the food material is selected for ingestion and then passed on to the mouth. Unsuitable material is passed to the bottom of the buccal cavity and permitted to fall out between the third maxillipeds. This is mainly large inorganic particles. Ingestion of a small amount of coarse mineral material is apparently not harmful to the crab, for it can be rejected by the cardiac stomach if need be. However, the presence of a large quantity of coarse material, such as sand grains, may interfere with the preparation of food material for digestion by the small, closely-set teeth of the gastric mill. Such a condition does not appear to be present in crabs feeding on a muddy substratum, for it is unlikely that fine, ingested silt particles would interfere with the functioning of the gastric mill. Thus, although there is little selection against such fine inorganic particles during feeding, as evidenced by the large percentage of silt in the fecal pellets of mud-feeding crabs, selection does occur among crabs inhabiting areas having a coarse substrate.

One method by which food material is sorted from the coarse mineral fraction is described by Altevogt and termed the flotation process in the present discussion. It involves introduction of water into the buccal cavity to float light food and silt particles free from the heavier material. The lighter fraction is suspended in water and held between the mouthparts, especially between the maxillipeds, by capillary action, while the heavier particles are washed to the lower part of the buccal cavity. At the base of the third maxillipeds, outside of the buccal cavity, the rejected material forms a fluid ball which is subsequently removed by the minor chela.

The water required for the flotation process is pumped from the gill cavity out through the excurrent opening by action of the scaphognathite. Flooding the buccal cavity, the water flows by gravity around the first maxilliped endopodite flaps and over the mouth parts. The reverse beat of the scaphognathite pulls a portion of the water back from the buccal cavity, while the remainder can return by way of the incurrent opening at the base of the branchiostegite. As the water is withdrawn, many of the fine, suspended particles adhere by capillary action to the mouth part surfaces, particularly to those covered with plumose hairs. Also, fine particles adhere to the two pairs of comb surfaces within the buccal cavity. The remainder of the suspended particles will be retained either by the plumose hairs fringing the distal flaps of the first maxilliped endopodites as the respiratory water is further withdrawn anteriorly, or by a similar fringe at the base of the third maxillipeds if the water passes out by that route. Experimentally, the flow of respiratory water into the buccal cavity can be stimulated by placing a flake of pablum on the first maxilliped endites. This reaction may be a result of weight on the bristles of the endites, or perhaps the bristles have gustative sensory properties.

This sorting process, which utilizes the difference in weight between the fine food material and coarse mineral matter as a criterion of selection, is supplemented by the coordinated actions of the mouth parts. These appendages hasten sorting by passing the food accumulated on their various combs and hair-covered surfaces on to the mouth, as well as by aiding to rid the buccal cavity of the larger and heavier material. The mouth parts also appear to be capable of freeing food material from the coarse particles, which increases the efficiency of the sorting process.

Food material is passed between the third maxillipeds and into the buccal cavity by the minor chela at a point near the tips of the endopodite palps. The tips of the palps lift outward and the endopodite plates swing open and lower slightly to make room for the food behind their broad, curved surfaces. The palps then return to their normal position and the endopodite plates partially flex closed, pressing the material up toward the first maxillipeds. The palps, aided by long hairs projecting from their tips, may also assist in pushing the material upwards.

Sorting by the mouth parts begins as the material is moistened by respiratory water. The particular role of the first and second maxillipeds in the feeding process varies with the type of substratum on which the crab feeds. *Uca pugilator* typically inhabits protected sandy tidal areas. When the crab feeds on the sandy substrate, relatively little food material is placed in the buccal cavity by the minor chela in proportion to the number of sand particles. Also, much of this food material clings to the sand grains, rather than being freely suspended in the interstitial water. Thus the feeding process involves more than merely a separation of the heavy mineral fraction from the lighter material, as is achieved by the flotation process. Rather, if the crab is to obtain a very large amount of food, it must be capable of removing from the mineral particles any food material which clings to them. The efficiency of the feeding process depends on the thoroughness and rapidity with which this is achieved.

The cleaning of adhering food material from sand grains is achieved in part, in *U. pugilator*, by modification of the bristles on the basal endites of the first maxillipeds. In general, the bristles are considerably enlarged, appearing quite stout and stubby. Toward the more median half of the endite they are broadened and flattened, with two edges of the bristles lobed from the base. The lobes curve inwards slightly to make the bristles cupped. Thus, the first maxillipeds of *U. pugilator* present an irregular surface against which sand grains may be scraped and food consequently removed as the second maxillipeds sweep the grains toward the sides of the buccal cavity. The bristles on the upper portion of the endites are set with their broadened surfaces perpendicular to the arc circumscribed by the second maxillipeds, permitting food material to accumulate on the broad, cupped surfaces as it is freed from the sand. The bristles on the lower portion of the endites have their cupped surface turned upwards, which enables them to catch any fine material washed down by the flotation process. In addition the modified bristles also serve to brush fine material from the first maxilliped endopodite combs which underlie them.

The cleaning process is also facilitated by similar modifications of the tips of some of the hairs on the meropodite of the second maxillipeds. These hairs are generally referred to as spoon-tipped. A spoon shape is achieved by the tips broadening and becoming shallowly cupped as the lobes near the tip arch inwards. There are five or six large lobes fringing two sides of the hair near the tip, in addition to a wide terminal lobe which is turned down over the tip to complete the cup. As the hair narrows proximally, it is fringed by several small lobes which grade into a series of serrate projections that soon become a mere fringe continuing along two sides of the shank for approximately half its length. These modifications make the hairs capable of effectively drawing large particles across the first maxilliped endites.

Though some spoon-tipped hairs are present on the second maxilliped meropodites in all species of *Uca* considered here, it is in *U. pugilator* that the highest degree of hair-tip modification is found. This is true both in the number of hairs which are spoon-tipped, and in the size of the modified tip. Almost all the medianly-projecting hairs of the meropodite in *U. pugilator* are modified (Plate I, Fig. 1). The short hairs covering the surface of the segment create a surface of stout, cupped bristles very similar to that described on the first maxilliped basal endites. This surface extends beyond the inner edge of the segment as the hairs become longer, with the more median hairs of the meropodite projecting well into the buccal cavity. As the hairs increase in length, the depth of the spooned portion and the extent of lateral lobing increases slightly. Proceeding posteriorly along the length of the meropodite, the hairs in each row decrease in length so that the spoon-tips are arranged in diagonal rows, which places the broadened hair-tips closely together to produce a continuous surface. While the spoon-tipped hairs extending from the second maxilliped meropodite of *U. pugilator* vary in number among individuals, it may be generally stated that there are close to one hundred spoon-tipped hairs which project beyond the inner edge of the meropodite in the smaller crabs. In the larger individuals over two hundred such hairs may be present on the meropodites. The shorter modified hairs, which do not project beyond the inner edge of the meropodite, range in number from seventy to one hundred in this species.

The spoon-tipped hairs on the second maxilliped of *U. pugilator* are believed to function primarily in the feeding process. Although some of the sand taken into the buccal cavity will fall to the base of the third maxillipeds because of its weight, as the cavity is flooded with respiratory water, many of the grains become lodged among the bristles of the first maxilliped endites, particularly the long bristles fringing the coxal endite. It is this sand which is picked up between the modified hair-tips of the meropodite and swept across the bristled endites of the first maxillipeds, resulting in rapid and efficient removal of adhering food material. The sand grains are usually too large to be carried individually by a spoon-tip; instead, a grain is caught between neighboring spoon-tips, where it is firmly held as the close mat of broadened tips exerts pressure from the sides, and the stiff underlying hairs prevent the grain from falling through the mat. Thus, the spoon-tipped hairs, when placed closely together, appear to contribute to the feeding process by providing an enlarged surface of stout hair-tips which can prevent sand grains from being forced up into or through the meropodite hairs when the second maxilliped moves across the bristles of the first maxilliped endites. Such a surface appears necessary in crabs which feed on a sandy habitat, for with loss of sand grains from the surface of the bristled endites only a small percentage of sand would be cleaned and little food material would be recovered. Food freed by the cleaning process is of a very light and filmy texture, which readily adheres to the modified bristles of the first maxilliped endites and the fringes and spoon-tips of the second maxilliped meropodite hairs. Little food accumulates in the spooned portion of the second maxilliped hairs, but it is apparently passed directly to the first maxilliped endites as the meropodite moves over them.

In addition to facilitating the cleaning of organic material sand grains, the sweeping action of the second maxillipeds across the buccal cavity also serves to carry coarse particles away from the central portion of the cavity. This can be considered as another general role of the second maxillipeds and of the spoon-tipped hairs in feeding. Once the particles have been carried to the sides of the buccal cavity, the meropodites lift away from the first maxilliped endites, which permits the sand to fall from the appendages as a vibratory action of the second maxillipeds and the flooding of the buccal cavity with respiratory water provides impetus to free the grains from the hair surfaces. The utilization of water to remove coarse particles from the buccal cavity is suggested by the fluid consistency of the ball of sand which accumulates at the base of the third maxillipeds for discard.

On the maxilliped meropodite of the marsh fiddler crab, *U. pugnax,* fewer of the medianly-projecting hairs are spoon-tipped, as compared to the sand-inhabiting species, *U. pugilator*. Also, in *U. pugnax* the modified hairs are limited to the upper portion of the meropodite (Plate I, Fig. 2). There are several rows of shorter hairs which do not project beyond the edge of the meropodite and which are well-lobed and broadened, but they are of a soft texture, which makes their effectiveness in manipulation of material questionable. However, there are five or six additional diagonal rows of stout, spoon-tipped hairs which extend beyond the meropodite, of a size and shape very similar to the spoon-tips in *U. pugilator*. The thirty to forty modified hairs in *U. pugnax* are not as closely grouped as in *U. pugilator*, somewhat decreasing the effectiveness of the narrow band of spoon-tips in picking up material. The band of spoon-tipped hairs does coincide in position with the upper edges of the first maxilliped endites in *U. pugnax*. Thus, the second maxillipeds appear to aid the feeding process primarily by picking up coarse particles from those edges of the endites and sweeping them away from the central portion of the buccal cavity. It is doubted whether as much food material is scoured from the coarser particles as a consequence of this action as in *U. pugilator*, for the bristles covering the first maxilliped endites of *U. pugnax* are not stout, but have a fine, downy texture.

The thoroughness with which the crabs are able to sort food from the mineral fraction of the substratum corresponds to the availability of food material. On the sandy beach inhabited by *U. pugilator*, while some detritus and nematodes are present in the interstitial water, much bacteria and algae is on the surface of the grains. This crab appears to ingest a minimal amount of sand and the food must therefore be separated from the mineral fraction. For the marsh-inhabiting *U. pugnax*, on the other hand, food is more readily available because the silt with which it is generally associated is of sufficiently fine texture to be ingested.

In *U. minax*, modification of the second maxilliped hairs occurs to a much lesser extent than that observed in either of the other two species. There are very few short hairs present along the upper surface of the meropodite and they are mostly limited to its edges. The modification observed in many of the medianly-projecting hairs consists of a feathering of two sides of the hair, the increase in surface adapting it to handle fine particle matter. In addition, in the larger crabs, many of the longer medianly-projecting hairs are hooked at their tip. In the more medium-sized crabs (of approximately 13.0 mm. to 19.0 mm. carapace width) these hair tips are microscopically flattened, with delicate lobes fringing the two sides of the flat surface near the tips, which then blend proximally into the serrulate projections that feather the shaft. Also, among the medium-sized crabs, several of the longer hairs of the meropodite are spoon-tipped, although in *U. minax* the spooned portion is much smaller and accordingly more shallow than those previously described (Plate I, Fig. 3). The spoon-tipped hairs extend medianly from the upper portion of the meropodite as three or four diagonal rows, each consisting of five modified hairs. These fifteen to twenty-four spoon-tipped hairs form a narrow band in the same position under the first maxilliped endites as in *U. pugnax*. However, in *U. minax*, the spoon-tips are widely spaced and are believed capable of doing little more to supplement the manipulation of material than what is typically achieved by the medianly-extending rows of unmodified hairs.

The presence of only a few modified hairs in *U. minax* is significant in view of the greater availability of food in the high marsh. Since *U. minax* can readily obtain the food associated with the finely sorted muddy substratum or on partially decayed marsh vegetation, there is neither a need for a highly efficient method of sorting food nor a systematic means of ridding inorganic material from the buccal cavity. It is probable that the medianly-projecting hairs contribute to the feeding process merely by dispersing material across the endites of the first maxillipeds, whereby a larger percentage of the particles within the buccal cavity are exposed to washing and respiratory water and food material is more readily separated for ingestion.

In all three species of *Uca* considered here, the last two segments of the second maxilliped palps are fringed with stout spoon-tipped hairs along their lower edge. The modified hairs of the terminal segment have their cupped surfaces facing downwards, while the spoon-tipped hairs of the propodite have the cupped surfaces turned inwards. So placed, the short, well-lobed hairs make the flexible palps very effective in manipulating material within the buccal cavity. In addition to facilitating removal of material from among the mouth parts, these hairs also enable the palps to collect food material which is accumulated on the hairy surfaces of the mouth parts, such as on the first maxilliped endites, or the fringes of plumose hair on the outer edges of the second maxillipeds, where it is deposited after the flotation process. The palps then carry the food to the maxillae, where it is closer to the mouth. The spoon-tipped hairs are conspicuously abundant on the palps of *U. pugilator*, while in the other two species they are somewhat fewer in number and less deeply curved. Yet the basic arrangement of these spoon-tipped hairs remains fairly consistent among the three species, indicating the importance of the palps in performing these functions in the feeding process, regardless of the character of the substratum on which the crab normally feeds.

The second and first maxillae work together to accumulate the finer material for ingestion. The upper pairs of endite lobes of the second maxilla appear to serve primarily to retain food material as it is sorted from the coarse particles, for they are abundantly covered with plumose hairs of moderate length. Underlapping these second maxillae endite lobes are several spoon-tipped hairs which project from the anterior edge of each first maxilliped basal endite. It appears that the hairs are modified primarily to function as surfaces against which the plumose surfaces of the second maxilla can rub, for the lateral movements made by the maxilla as the scaphognathite moves within the gill cavity do move the basal endites against these first maxilliped hairs. With this action, any fine material caught in the plumose hairs of the basal endite of the second maxilla will be carried toward the median edge of the segment, where it is in a position to be passed on toward the mouth. There are also a few hairs which project anteriorly from the second maxilla, which are similarly hooked. Likewise, these hairs would move fine material to the median edges of the first maxilla basal endites which lie above them. There is little species difference in the form or arrangement of the hair modifications discussed here.

Food material is removed from the median edge of the second maxilla basal endite as the segment moves posteriorly and upward, scraping its plumose surface against the anterior edge of the coxal endite of the first maxilliped. This action places the fine material above the first maxillipeds and in a position to be carried to the maxillary combs by respiratory water. In addition, food can be passed from the first maxilla basal endites to the tufted edges of the mandibular palps, as the mandibles move laterally above the endites. This material also appears to be carried from the palps to the maxillary combs as the mandibles are washed with respiratory water.

The combs of the second maxillae curve medianly from the base of the coxal endites, closely adhering to the bristled, convex surface of the first maxilla coxal endites. The combs appear to serve as surfaces to retain material carried into the upper portions of the buccal cavity by the flotation process. The maxillary comb and brush surface of the coxal endite of the first maxilla appear to perform the same function as that described for the first maxillipeds; however the comb and brush surfaces of the maxillae appear to be capable of handling finer material since the hairs of these surfaces are set closer together. The fine food material and silt on the combs are transferred to the median edges of the first maxilla coxal endites as the endites brush the convex combs beneath them. As food material accumulates near the median edge of the bristled surface, the first maxilla can move forward a short distance, placing the inner edge of the coxal endite, and the food material, in the mouth.

Disscussion

Certain aspects of the feeding mechanism of *Uca* help to explain the ecological limitations imposed upon the crabs by their mode of feeding. Analysis of the feeding mechanism shows two general processes to be involved: flotation, and coordinated action of the mouth parts. Considering the flotation process, it is instructive to examine the copious use of water from the gill cavities of the crabs in light of water conditions prevailing in their respective habitats. After the flooding of the buccal cavity with respiratory water, some water is returned to the gill cavities, either via the excurrent openings as the scaphognathite reverses its direction of movement, or by way of incurrent canals, located at the base of the branchiostegite above the coxa of the chelae. The latter route was suggested by Altevogt. However, some water is lost as food is ingested, as well as when material is discarded from the buccal cavity. Additional water is lost by evaporation while the mouth parts are exposed to the air. Thus, to continue feeding, the crab must have access to an external supply of water in order to replenish its respiratory water. This factor is important in limiting the areas where the crabs may feed, and is reflected by the moist condition of the material from which they prefer to feed. Of more general significance, the inclusion of the flotation process as an integral part of the feeding mechanism is one major factor preventing *Uca* from living in a terrestrial habitat.

Among the marsh-inhabiting fiddler crabs, the requisite of standing water for the flotation process affects its distribution little, other than limiting the crab to the intertidal areas, for within that area the substratum remains moist and water is available even during low tide in drainage depressions and in the depression surrounding the burrow entrance. *Uca* can readily replenish its respiratory water from such small pools by lowering the thorax into the water, submerging the incurrent canals at the base of the branchiostegite. *U. pugnax* has been observed to stray from its burrow while feeding and to lower its thorax to take up additional water, only to find the moisture insufficient. Immediately the crab returned to its burrow, where it could take up water, and then once again it began feeding. This relationship between the burrow and a source of respiratory water may be a key factor contributing to the high sense of burrow-centered territoriality which has been observed in *U. pugnax.* That such territoriality has not been observed with *U. minax* is in agreement with its preference for feeding in the muddier portions of the marsh, away from the burrowing area.

In the sandy areas inhabited by *U. pugilator,* the need of water for the flotation process has a more pronounced effect on the movements of the crab. As well as being limited to the moist intertidal portion of the protected beach, the crab may also be required to move to the water's edge to feed, should the beach elevation at the burrowing area be too great for water to remain in the burrow during low tide. Both the tidal magnitude, as influenced by the phase of the moon and the season of the year, and the contour of the beach, will affect the water level, and thus be factors contributing to vertical movements of the crab during feeding.

Ecological considerations may be deduced by examining the role of the mouth parts in feeding. Generally speaking, the mouthparts manipulate material within the buccal cavity by two coordinated actions: that which passes food material toward the mouth and one which removes coarse material from the central portion of the buccal cavity. Species differences are observed in the hairs covering the mouth parts in *Uca*, which reflect the relative importance of the several mouth part actions in the feeding process of each species. Since the majority of these mouth part differences can be correlated with the type of substrate on which the crabs typically live, they can be looked upon as modifications which enable the crabs to feed in that habitat.

Of the three fiddler crabs considered here, the mouth part hairs of *U. minax* appear to be the least modified, it being assumed that the undifferentiated hairs are the more primitive. This species typically lives in the mature *Spartina* marshes, well up the estuary where lower salinities are experienced. Field studies indicate that *U. minax* prefers to feed in low areas where the mud is very fluid. The crab also feeds extensively on bacterial slime on decaying plant material, which is abundant throughout the marsh. The material carried to the buccal cavity by the minor chela is generally of such a fine texture that little sorting would be required by the mouth parts before ingestion could take place. Respiratory water is still pumped into the buccal cavity, however, where it doubtless serves as a solvent aiding in the dispersal of the fine material to the various mouth parts. Once on these hair-covered surfaces the mouth parts pass the fine silt and food material upwards to the mouth.

Should material be rejected from the buccal cavity during feeding in *U.minax,* rejection occurs immediately after the material is placed within the cavity, and all is discarded. Since rejection takes place without sorting, the palps of the second maxillipeds, rather than respiratory water, would serve to direct the material from the buccal cavity. The palps also aid in the manipulation of particles within the cavity, for which they are particularly adapted due to the arrangement of the spoon-tipped hairs on the terminal segments. A similar modification occurs with the longer, medianly-extending hairs of the meropodite, although here it is limited to a minute hooking or flattening of the tip, which is fringed by delicate lobes and setules. These long hairs may increase the efficiency of the sorting process by spreading the material across the first maxilliped endites, where it will be more accessible for washing by respiratory water, as well as providing another surface on which fine material may accumulate.

The presence of flat-tipped hairs on the second maxilliped meropodites in *U. minax* is felt to be a modification serving to increase the efficiency of the sorting process and to enable crabs to invade and survive in intertidal areas having a coarser substrate, where food material is not readily available. A slight advancement in this direction is seen with the modification of a number of hair tips to a deeply spooned shape in *U. pugnax*, with an accompanying ability of the crab to feed in sandy portions of the marsh. The modified hairs, which may approach thirty in number, extend from the upper portion of the second maxilliped meropodites, where they are effective in removing coarse material from the upper edges of the first maxilliped endites and withdrawing material from the central part of the buccal cavity. The spoon-tipped hairs present on the second maxilliped palps are similarly arranged in both *U. pugnax* and *U. minax,* as is also the luxuriant fringe of plumose hairs on the outer edges of the second maxillipeds and on the maxillae, which basically adapts *U. pugnax* to feed on a muddy substrate.

The greatest modification of the hairs of the mouth parts appears in *U. pugilator*. Here the terminal lobing of the spoon-tipped hairs is more pronounced, making the tips more rounded and deeply cupped, which, coupled with the greater number of spoon-tipped hairs present, greatly increases the efficiency of the mouth parts in handling coarse material. The most striking surfaces of closely set spoon-tips are those formed by the hairs extending medianly from the meropodite of the second maxillipeds. The number and size of the spoon-tipped hairs of the second maxilliped palps are also increased in *U. pugilator,* making those two opposing surfaces of spoon-tipped hairs on the dactylopodite and propodite more effective. Thus the palps further supplement the action of the meropodite in manipulating material to be discarded from the buccal cavity, as well as carrying accumulations of food to the maxilla for passage to the mouth. This efficiency in handling coarse material within the buccal cavity enables the crab to feed in such habitats as the protected sand beach.

In addition to the necessity of selecting against coarse mineral particles, another problem which appears to confront fiddler crabs living in a sandy habitat is the paucity of available food material, for there the organic matter is closely associated with the coarse sand. In such a form, the food material is not as readily available for ingestion as is the organic matter in the marsh, which is associated with fine silt. Thus, a beach-inhabiting fiddler crab must also be capable of efficiently separating from the sand a large percentage of the food material which is taken into the buccal cavity. In *U. pugilator,* the efficiency of the sorting process is increased by a cleaning action which involves the drawing of sand particles over the bristled surface of the first maxilliped basal endites by the second maxillipeds. The bristles of the basal endites are modified in *U. pugilator* in a manner similar to that of the tips of many of the hairs on the second maxillipeds. Such enlarged bristles projecting perpendicularly from the endites offer a brush-like surface against which sand grains may be scraped and food material removed as the second maxillipeds sweep the grains across the endites. The bulk of the freed food is then retained on the shallowly-cupped endite hairs, which are placed in such positions as to catch the maximum amount of loose food material which may be washed toward the base of the buccal cavity by respiratory water. The closely set spoon-tipped hairs of the second maxilliped meropodites facilitate this cleaning process by providing a sufficiently rigid surface to achieve efficient scouring action on the sand grains as they are carried across the first maxillipeds.

Distribution of *Uca* is generally believed to be governed by a complex of physical and biotic factors, operative during the pelagic developmental stages of the crab, as well as after it has invaded the intertidal areas. However, in considering the influence of the observed modifications of the mouth part hairs on the distribution of *Uca,* only the adult crabs and their intertidal habitat need be examined, for it is only in the adult stage that the mouth-part hairs are well developed, and thus fully functional. In *U. minax,* the condition of the mouth-part hairs indicates that they are not able to sort food material from coarse inorganic matter with any efficiency. This leads to the inference that the crab would be able to survive only in areas where it has access to an abundance of food material on the surface of a silty substratum, such as in the salt marsh. However, *U. minax* does not inhabit all portions of the tidal marsh, but it is generally restricted to the high regions, where a dense mat of *Spartina alterniflora* roots and rhizomes impart great stability to the substrate. In view of this restricted distribution within the marsh, though nutritive conditions appear fairly consistent throughout, there are doubtless limiting factors other than an inability of the crab to obtain food. It is probable that the stability of the substrate, which differs from that of the lower marsh, is critical for the crabs' burrowing activities.

The more advanced modification of some of the hairs on the mouth appendages in *U. pugnax* does appear to be an adaptation permitting the crab to be more widely distributed. This is demonstrated by the crabs' presence in the sandy areas of young marshes. There feeding is facilitated by the band of modified hairs extending from the upper portion of the second maxilliped meropodites, which can manipulate coarse material in the central region of the buccal cavity. The inability of *U. pugnax* to survive on protected sandy beaches, however, where surface food material is less available, reflects on the unmodified condition of the first maxilliped basal endites and the wide spacing of the spoon-tipped hairs present on the second maxilliped, which limits the efficiency with which food can be cleaned from the coarse grains. Thus the lack of modified hairs is one factor limiting *U. pugnax* to marshy areas, where food material can be more readily obtained.

The ability of *U. pugilator* to obtain sufficient food from its sandy habitat is seen to lie principally in the highly modified condition of the first and second maxillipeds. However, it is difficult to believe that this structural adaptation renders the crab incapable of surviving in marshy areas, particularly when its presence in the sand-fringed young marsh is considered. There *U. pugilator* inhabits primarily the high sand rim when it is flooded by a spring tide. During the neap tides, when the high sandy areas remain dry, the crab moves into the siltier areas of the marsh where the surface substratum may contain only 40% sand. With the next spring tide, a large portion of the population returns to the sand fringe, demonstrating an apparent preference for the sandier areas. Population pressure may play a role in this latter movement, for when *U. pugilator* is in the silty marsh areas, it shares the space with *U. pugnax*. But more generally, the ability of *U. pugilator* to feed with efficiency in a sandy area is looked to as a basis for this preference. When the crab feeds from a sandy substrate, the inorganic fraction of the material passed into the buccal cavity is of sufficient size that it may be readily discarded during the sorting process, and little inorganic material is ingested. This, coupled with the effective cleaning process in *U. pugilator,* indicates that material of a relatively high total nutritive value is ingested during feeding. In the marsh, however, the efficiency of the feeding process is diminished, since the silt with which the organic matter is associated is of too fine a texture to permit separation of the food material. This is further borne out by examination of the fecal material of *Uca,* which indicates that these fiddler crabs do not remove fine silt from the organic matter. Therefore, in the marsh the nutritive value of the material ingested by the crab is reduced in comparison to that of sand-inhabiting species. While observations show *U. pugilator* to be capable of surviving in areas with little sand in the substratum, the mouth part modifications which have aided it in surviving in sandy areas have also exposed it to such advantageous nutritive conditions that the sandy habitat has become the more favorable. However, since this factor appears to be more of a preference than an absolute requirement, there are probably other factors, such as the consistency of the substratum for burrowing, which prevent *U. pugilator* from living in the marsh.

Summary

1. A study has been made of the feeding mechanism of three species of fiddler crabs: *Uca pugilator, U. pugnax* and *U. minax.*
2. Fiddler crabs feed by scraping organic matter from the surface of the substratum, with subsequent separation of food material from the coarser fraction within the buccal cavity.
3. The two basic aspects of the feeding mechanism are the coordinated actions of the mouth parts and a flotation process which utilizes water from the gill cavities.
4. Species-specific modification of the hairs which cover the mouth parts are described and correlated with the characteristic substratum on which each species feeds.
5. The distribution of the fiddler crabs is discussed, with consideration of ecological adaptations of the feeding mechanism within each species.

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EXPLANATION OF THE PLATE

PLATE I

FIG. 1. Median portion of the right second maxilliped meropodite, *U. pugilator,* dorsal view.

FIG. 2. Median portion of the left second maxilliped meropodite, *U. pugnax,* dorsal view.

FIG. 3. Median portion of the right second maxilliped meropodite, *U. minax,* dorsal view.